ANIMALS AND ECOSYSTEM FUNCTIONING

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INTRODUCTION

Soil animals (i.e., fauna) are represented by a diverse array of creatures living in or on soil for at least a part of their life cycle. Many animals have influences on soil properties, but should not be considered soil dwellers since only a minor portion of their life cycle is spent in the soil (Fig. 1).

Based on body size, soil animals can be divided into three categories:

1. microfauna (<200 μm length, <100 μm width) including protozoa, rotifers, and nematodes
2. mesofauna (0.2–10 mm length, 0.1–2 mm width) including tartigrades, collembola, and mites
3. macrofauna (>10 mm length, >2 mm width) including millipedes, spiders, ants, beetles, and earthworms

Soil animals can also be classified according to where they inhabit the soil. The aquatic fauna (e.g., protozoa, rotifers, tartigrades, and some nematodes) live primarily in the water-filled pore spaces and surface water films covering soil particles. Earthworms are divided into species that occupy the surface litter of soil (epigeic), that are found in the upper soil layers (endogeic), or that burrow deep into the soil profile (anecic).

A further classification of five groups of soil animals is based on feeding activity, which can be useful in distinguishing how different groups affect soil ecosystem functions:

1. Carnivores feed on other animals. This group can be subdivided into: i) predators (e.g., centipedes, spiders, ground beetles, scorpions, ants, and some nematodes), who normally engulf and digest their smaller prey and ii) parasites (e.g., some flies, wasps, and nematodes), who feed on or within their typically larger host organism.
2. Phytophages feed on living plant materials, including those that feed on above-ground vegetation (e.g., snails and butterfly larvae), roots (e.g., some nematodes, fly larvae, beetle larvae, rootworms, and cicadas), and woody materials (e.g., some termites and beetle larvae).
3. Saprophages feed on dead and decaying organic material and include many of the earthworms, enchytraeids, millipedes, dung beetles, and collembola (or springtails). Saprophages are often referred to as scavengers, debris-feeders, or detritivores.
4. Microphytic feeders consume bacteria, fungi, algae, and lichens. Typical microphytic feeders include mites, collembola, ants, termites, nematodes, and protozoa.
5. Miscellaneous feeders are not restrictive in their diet and consume a range of the previously mentioned sources of food. This group includes certain species of nematodes, mites, collembola, and fly larvae.

The arrangement of these feeding groups can be visualized as a soil food web with multiple trophic levels, beginning with the autotrophic flora (Fig. 2). Trophic levels describe the order in the food chain. The first trophic level is composed of photosynthetic organisms, including plants, algae, and cyanobacteria, which fix CO_2 from the atmosphere into organic compounds. Organisms that consume the photosynthesizers are in the second trophic level, which includes bacteria, actinomycetes, fungi, root-feeding nematodes and insects, and plant pathogens and parasites. The third trophic level feeds on the second trophic level, including many of the dominant soil animals, including bacterial- and fungal-feeding arthropods, nematodes, and protozoa. The soil food web can be continued to include various vertebrates, including amphibians, reptiles, and mammals.

SPATIAL DISTRIBUTION OF SOIL ANIMALS

Soil animals are not uniformly distributed in soil. Unlike the soil microflora, which could be considered ubiquitous, the proliferation of soil animal communities is more sensitive to environmental disturbances and ecological interactions. Gross climatic differences afford opportunities for unique assemblages of organisms. Even within a specific climatic region, large differences occur in the community of organisms present based upon type of

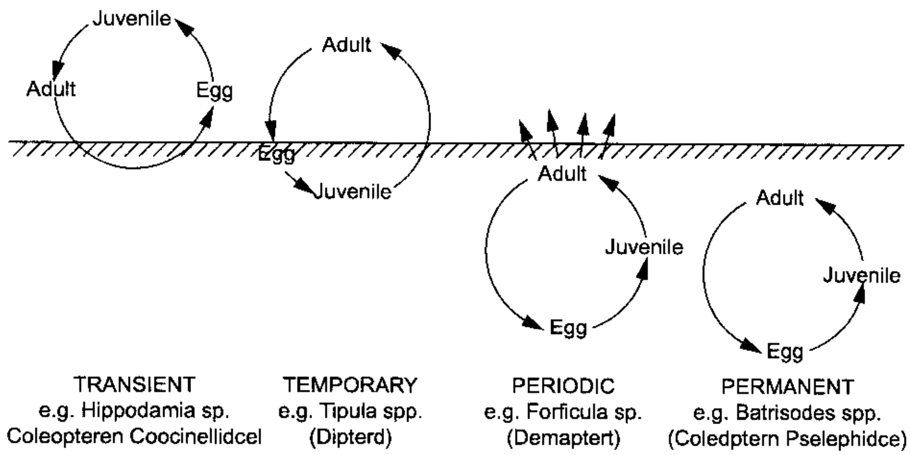

Fig. 1 Categories of soil animals defined according to degree of presence in soil, as illustrated by some insect groups. (From Ref. 1.)

vegetation, soil, availability of water, land use, and presence of xenobiotics. Within the confines of a seemingly uniform pedon, "hot spots" of soil organism activity can be isolated based on localized availability of resources and environmental conditions (Fig. 3).

INFLUENCE OF SOIL ANIMALS ON SOIL FUNCTIONS

Decomposition and Nutrient Cycling

Soil animals work directly and indirectly with the soil microflora (i.e., bacteria, actinomycetes, fungi, and algae) to decompose organic matter and mineralize nutrients (3). The primary consumers of organic materials are the soil microflora. Soil animals, like many of the microflora, are heterotrophs and therefore consume organic materials to gain energy for growth and activity. Soil animals make important contributions to decomposition by

1. shredding organic materials, thereby exposing a greater surface area for enhancing the activities of other organisms, especially microorganisms;
2. consuming resistant plant materials that would decompose slowly otherwise, such as wood, roots, and dung, and transforming these materials into more decomposable constituents;
3. dispersing soil microorganisms (i.e., inoculation) within the soil profile by transporting them on their bodies and through their intestinal tracts;
4. creating burrows in soil to increase aeration, which stimulates microbial activity;
5. transporting organic materials from the soil surface to deeper in the soil profile, thereby improving environmental conditions for decomposition and increasing biological interactions deeper in the soil profile;
6. consuming bacteria and fungi, thereby releasing nutrients and stimulating the regeneration of microbial populations; and
7. providing unique food sources themselves for consumption by other soil fauna and microflora.

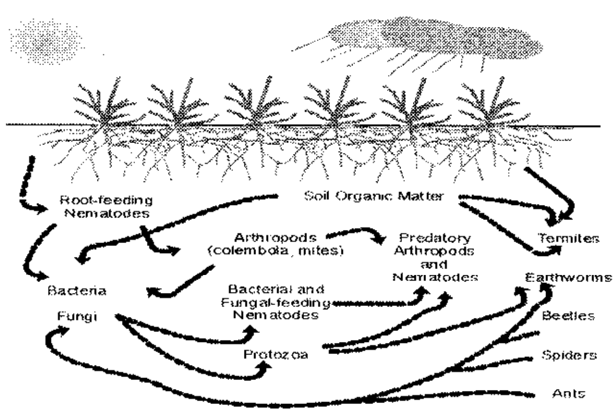

Fig. 2 Generalized diagram of a soil food web.

Water Cycling

Soil animals are active participants in the formation of soil structure, which is an important characteristic that influences water infiltration, soil water retention, and percolation (4). The biochemical activity of soil organisms transforms organic materials into soil-stabilizing cementing agents, which bind the primary soil particles (i.e., sand, silt, and clay) into aggregates. In addition, the burrowing

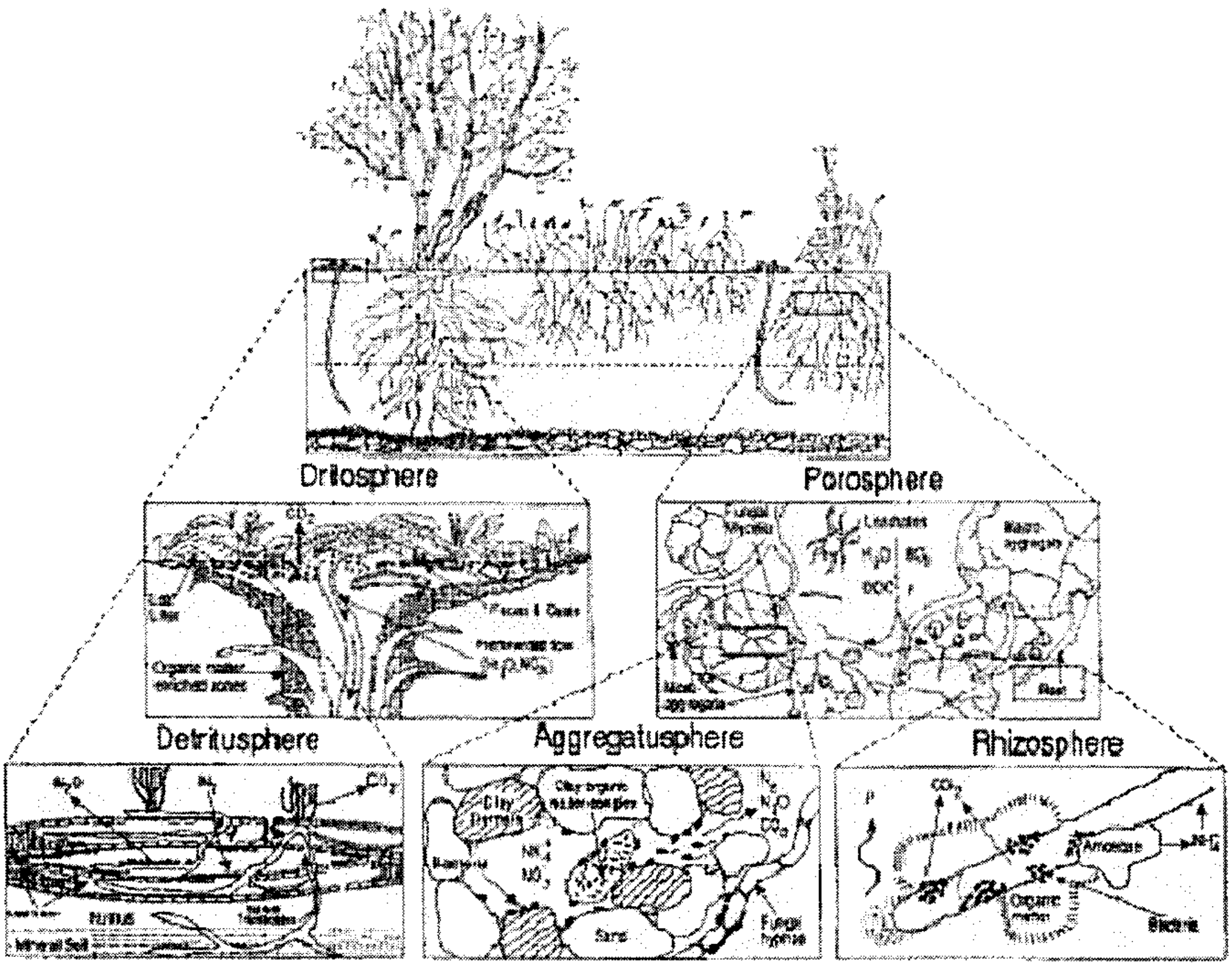

Fig. 3 Key locations of soil organism activity. (From Ref. 2. with kind permission from Kluwer Academic Publishers.)

activity of soil animals creates larger pores alongside water-stable aggregates to increase total porosity of soil, which aids water flow without decreasing overall water retention capacity and improves the plant rooting environment.

Both aggregates and porosity are important components of soil structure. Poor soil structure due to disruption of aggregates, which fills pores with disaggregated primary particles and causes crusting of the soil surface, results in more rainfall that runs off land (i.e., less infiltration), potentially carrying with it sediment, nutrients, and pesticides that can contaminate surface waters. Reduced infiltration with poor aggregation reduces available water for plant growth (i.e., reduces net primary productivity and the potential to fix atmospheric CO_2) and reduces percolation of water through the soil profile, essential for purification and recharge of groundwater.

Those animals that create burrows in soil also create conduits for water movement through the soil profile. These biopores can be important for improving water percolation and improving rooting below claypans and other restrictive soil layers.

Many different soil animals deposit fecal pellets, which become stable soil aggregates when the organic material is mixed with soil mineral particles. These aggregates are able to retain more water because of the high water-holding capacity of soil organic matter.

Pest Control

Intense competition among soil organisms keeps an ecosystem healthy by preventing one organism from becoming dominant. Potential plant pathogens, such as root-feeding nematodes, are often held below damaging levels because of consumption by predatory nematodes and arthropods. With a healthy food web rich in species diversity, the predatory activity of many arthropods can keep crop pests below economic thresholds.

Impact of Key Soil Animals

Earthworms

Earthworms are well-known soil animals inhabiting many environments, most prominently found in moist-temperate ecosystems. As earthworms ingest organic materials and mineral particles, they excrete waste as casts, which are a particular type of soil aggregate that is rich with organic matter and mineralizable nutrients. It is estimated that a healthy population of earthworms can consume and aerate a 15 cm surface of soil within one or two decades. Anecic or deep-burrowing species of earthworms can create relatively permanent vertical channels for improving root growth and water transport. Important attributes of earthworm activities are increased surface soil porosity, enhanced water infiltration and nutrient cycling, and distribution of organic matter within the soil profile to increase soil microbial activity.

Termites

Termites are important soil animals in grasslands and forests of tropical and subtropical regions. They often build mounds by excavating subsoil and depositing it above ground to build a city of activity with a complex social system. Termites are able to decompose cellulose in wood because they harbor various microorganisms (protozoa, bacteria, or fungi) to aid in decomposition. Better drainage and aeration of termite mounds may be beneficial to nearby plant growth in soils with a high water table. Stable macrochannels created by termites can improve water infiltration into soils that otherwise would form impermeable surface crusts.

Protozoa

Protozoa are single-celled animals that generally consume bacteria and soluble organic matter. Protozoa are more numerous in marine and freshwater environments, but do occur widely in water films of many soils (5). Their principal soil function is predation on soil bacteria, which releases nutrients for potential plant uptake; increases decomposition and soil aggregation by stimulating their bacterial prey; and prevents some bacterial pathogens from developing on plant roots.

SOIL BIODIVERSITY

There has been a great deal discovered about soils and the organisms that live in them, yet it is estimated that <10% of the species of soil organisms have been identified globally. A rich diversity of genetic information resides in soil. An awaiting challenge is to discover the ecological consequences of soil biodiversity. A critical understanding of how organisms interact has begun, yet there will be much more to learn about how species diversity interacts with functional diversity. There may be soil functions provided by organisms that we are unaware of even today.

How biodiversity relates to ecosystem functioning is an intensive area of current research in both above- and below-ground ecology (6, 7). Recent experimental evidence suggests that loss of species richness due to perturbations may not always lead to loss of ecosystem functioning, especially in initially species-diverse functional groups (8). Ecosystem functions can be performed by a number of different species within a trophic level, suggesting that functional redundancy is a mechanism to insure stability. However, loss of functional groups in trophic levels closest to the base of the detrital food web would be most detrimental to ecosystem stability. Future work on soil biodiversity should unravel the relative importance of species richness on the resistance and resilience of ecological processes under various short- and long-term stresses and environmental conditions.

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